18

Patterns of Tree Mortality in a Monodominant Tropical Forest

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1. Introduction

Tree death in forests is an important process at many ecological levels. The mortality rates of trees affect carbon and nutrient cycling, stand structure, community composition, and successional processes (van Mantgem et al. 2009). Tree death substantially increases resources such as light, nutrients, water, and energy available to other organisms. Dead standing trees (snags) provide important habitat for wildlife and dead fallen trees are often critical to seedling establishment as nurse logs (Franklin et al 1987). Despite their importance, the mechanisms that drive tree mortality are often unclear, especially in tropical forests (Swaine et al. 1987). There is particular lack of information on how both mortality and longevity varies with the species, individual size, and competition with the other trees. In order to predict the various impacts of global change on the dynamics of tropical forests, it is essential to understand the role these factors play on tree mortality at both the individual and landscape scale.

While most tropical forests have very high species richness, there are some in which a single species dominates and richness is fairly low. In many of these forests, monodominance may be perpetuated through periodic mortality as a result of massive, landscape-level disturbances such as volcanic eruptions, hurricanes, landslides, and fire (Connell and Lowman 1989, Hart 1990, Read et al. 1995). Like their more diverse tropical counterparts, the basic life-history characteristics of the species that comprise monodominant forests, particularly those related to mortality patterns, remain poorly understood.

Forests on oceanic islands in the tropics are often dominated by one or a few tree species (Mueller-Dombois and Fosberg 1998). The native, wet forests of the Hawaiian archipelago are generally dominated by a single endemic tree species, ohia (*Metrosideros polymorpha*). This tree forms monodominant stands from the earliest pioneer stages on recent lava flows to rain forest on substrates millions of years old (Atkinson 1970, Jacobi 1989, Gagne and Cuddihy 1990). In contrast to tropical forests in continental areas where gap phase dynamics plays a dominant role in succession (Denslow 1987), *Metrosideros* forest stands often occur in cycles, (*cyclic succession*) with generations of similar-aged canopy trees lasting from 300-500 years before they experience a canopy dieback event (Mueller-Dombois 1986). Pollen cores showing 2-3 pollen depressions per 1000 years (Hotchkiss 1998), and radiocarbon dating demonstrating non-overlapping age groups of canopy trees (Hart 2010), provide additional

support for this cyclic succession model. While the proximate causes of periodic cyclic mortality in *Metrosideros* are likely variable across the landscape, this pattern of mortality itself, where many, if not all of the trees in the canopy die at once, may help perpetuate monodominance in most Hawaiian forests.

Here, I use information from a long term study in permanent vegetation plots within 200 ha of monodominant Hawaiian wet forest to address the following questions: How does tree mortality vary with respect to species, size, position in the canopy (crown class), and geographic location? What is the age of trees in this forest? To what extent can patterns of mortality provide evidence for succession in this forest?

2. Methods

2.1 Study area and data collection

Fieldwork was conducted from January 1996-August 2005 within the 13,246 hectare Hakalau Forest National Wildlife Refuge on the eastern slope of Mauna Kea volcano, island of Hawaii (approx. 19º50N, 155º 20W). The Koa/'Ohi'a (*Acacia/Metrosideros*) Montane Wet Forest (Gagne and Cuddihy 1990) on this refuge is remarkably intact and is dominated by *Metrosideros* and *Acacia* trees that regularly reach 1m or more in diameter and heights greater than 30m (please see Hart 2010 for a further description of the study area). Like most other montane wet forests in Hawaii, federal and/or state laws prohibit logging, however invasive plant and animal species pose significant threats to native biodiversity. The substrate at Hakalau is generally comprised of silty clay (Akaka soil association; Sato et al. 1973) that developed in 10,000 – 30,000 year BP Tephra deposits (Wolfe and Morris 1996). Road cuts indicate that the soil is quite deep (greater than 3m in many areas) and relatively free of rock. Mean annual rainfall was approximately 2250mm at Hakalau during the study period. In 1996, two 100 ha study sites separated by approximately 4 km of continuous forest, were established at elevations between 1750 and 1900 m. Within each study site, 10 one km long transects were established with permanent 30m diameter circular plots (stations) placed at 100m intervals (200 plots total). From 1996-1998, all stems within each plot greater than 5 cm diameter at breast height (DBH) were marked with an aluminum tag secured to the tree with an aluminum nail at approximately 1.3 meters above the ground. The diameter of each tree (both live and dead) was measured with a synthetic fabric diameter tape at a point approximately 3 cm above the tag. In addition, all trees were classified as belonging to one of four distinct crown classes within the canopy stratum: dominant, co-dominant, intermediate, and suppressed (Smith 1986). Dominant trees generally had full sun exposure to the crown throughout the day. Co-dominant trees had full exposure to the top of the crown, but were partially shaded on the sides by other co-dominant or dominant trees. Intermediate trees were those in which the upper portion of the crown was shaded by neighboring trees for a portion of the day. Suppressed trees were generally completely shaded by neighboring trees throughout the day. From 2004- 2005, all tagged trees within each of the 200 survey plots were re-measured 3 cm above the aluminum tag, and changes in growth state (live to live vs. live to dead) were determined. Trees that had died between surveys were further characterized as "dead-standing" or "dead-fallen" to provide further evidence for cause of mortality.

2.2 Mortality rates

Annual mortality (m) was calculated following equation 6 of Sheil et al. (1995) as:

$$m = 1 - (N_1/N_0)^{1/t},$$

where 'N_0' and 'N_1' are population counts at the beginning and end of the measurement interval, and 't' is the mean number of years between measurements. Bootstrapped standard error estimates of annual mortality rates for each species were calculated using 1000 bootstrap replicates from the binomial distribution, where 'p' = observed annual probability of mortality and 'n' = sample size (Chernick 2008).

To model survival, I used a logistic ANCOVA (Crawley 2007) with growth state (live vs. dead) as a response variable and DBH and crown class, along with their interaction, as predictors. Four different models were constructed and ranked with Akaike's Information Criterion (AIC:Akaike 1973) using R software (version 2.12.1; The R Foundation for Statistical Computing). This model selection criterion is based upon the principle of parsimony and represents a tradeoff between model fit and the number of parameters in the model (Burnham and Anderson 2002). Deletion tests (Crawley 2007) were then used to cross validate the model selection procedure by assessing the significance of the increase in deviance that resulted when a particular term was removed from the full model. Deletion tests were run on model pairs using the *anova* function in R.

If mortality is associated with stand-level dieback in *Metrosideros*, it might be expected that there are discernable spatial patterns of mortality across the landscape. To address this idea, I used the proportion of trees that died during the study period at each station at the Pua Akala study area to calculate a Getis-Ord Gi* statistic (also known as a z score) using the Hot Spot Analysis tool in ArcGIS 9.2 (ESRI 2010). This statistic helps identify those clusters of points with values higher in magnitude than would be expected by chance, with 'z' scores near zero providing evidence that, in this case, there is little clustering of mortality across the landscape.

Mortality rates for *Metrosideros* were used to evaluate longevity estimates based on growth rates and radiocarbon dating (Hart 2010). Using plot data, I estimated that the overall density of large, living trees (> 50cm DBH) within the study areas is approximately 27 trees Ha^{-1}, then used a conservative, pooled, annual mortality estimate for these trees of 1.1% to construct mortality curves to predict the number of years that individuals in this cohort of large trees will persist. This value was then added to the median, minimum, and maximum age estimates for the smallest trees in this cohort (Hart 2010) to produce tree longevity estimates.

3. Results

A total of 480 of the original 6173 trees of all species greater than 5 cm DBH died over the course of the study. The mean number of years between measurements was 6.75. Total mortality (number of trees that died during the study divided by total number of trees) ranged from 6.4% for *Ilex anomala* and 7.1% for *Metrosideros* to 33.3% for *Coprosma ochracea*. Annual mortality (Sheil et al. 1995) varied with species, ranging from 0.98%/yr for *Ilex* and 1.1% for *Metrosideros* to 5.82 %/yr for *Coprosma* (Fig. 1). The high annual mortality for *Coprosma* may be an over-estimate due to small sample size for this species (n = 21).

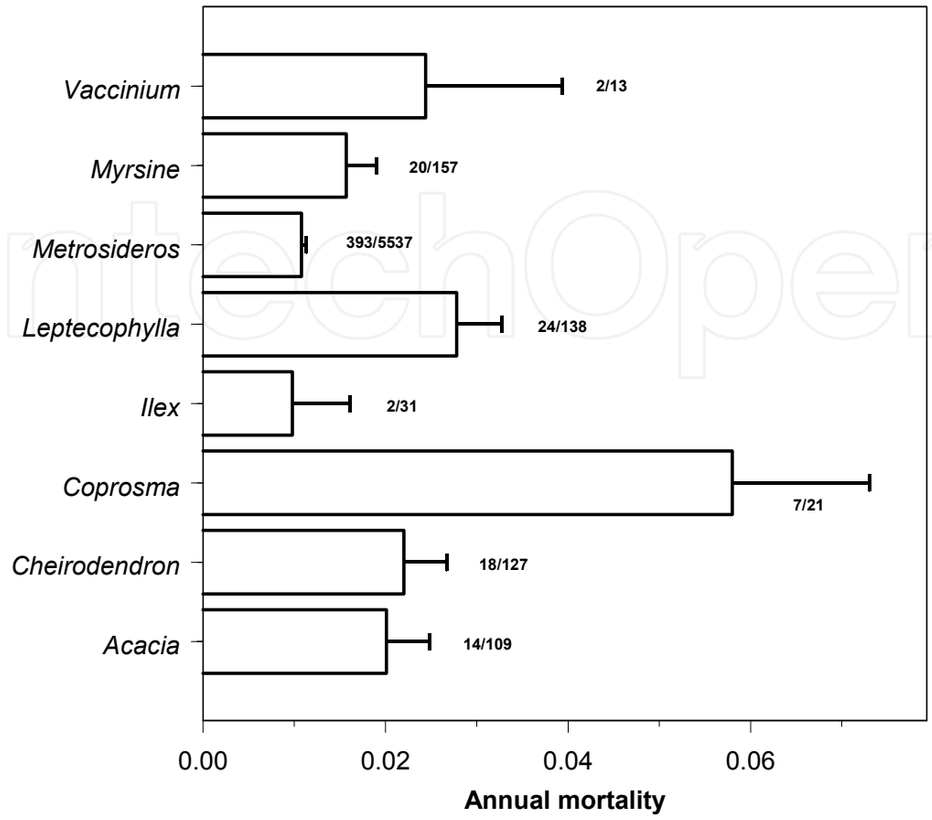

Fig. 1. Annual mortality for the eight most abundant tree species at Hakalau Forest NWR (*Acacia koa, Cheirodendron trigynum, Coprosma ochracea, Ilex anomala, Leptecophylla tameiameiae, Metrosideros polymorpha, Myrsine lessertiana*, and *Vaccinium calycinum*). Values above bars represent the total number of trees that died during the course of study vs. total trees examined for each species.

There was no evidence for any sort of clumped spatial patterns in *Metrosideros* mortality (Getis-Ord Z = 0.418, P = 0.675). The full logistic model that included crown class, tree size (DBH) and their interaction provided the best fit to the data for predicting whether a *Metrosideros* tree lived or died during the study (DBH: $df = 1$, $F = 117.04$, $P < 0.0001$; Crown Class: $df = 3$, $F=143.5$, $P < 0.0001$; interaction: $df = 3$, $F = 20.1$, $P < 0.0001$). This model had the lowest AIC value, and deletion tests of the model with vs. without the interaction term were highly significant, providing further evidence for the importance of the interaction term (Fig. 2).

For *Metrosideros,* percent annual mortality varied with size, ranging from 0.33% for trees 40-45cm DBH to 1.8% for trees between 10-15 cm DBH (Fig. 3). Annual mortality decreased with size between approximately 15cm – 45cm DBH, and again increased in the larger size classes (Fig. 3). When viewed by crown class category, suppressed trees accounted for much of the overall mortality, dying at a rate of approximately 3.8% per year (Fig.4). A Chi-square test on the frequency of mortality for each crown class category shown in Fig. 4 was highly significant ($\chi^2 = 298.2$, df = 2, $P < 0.001$).

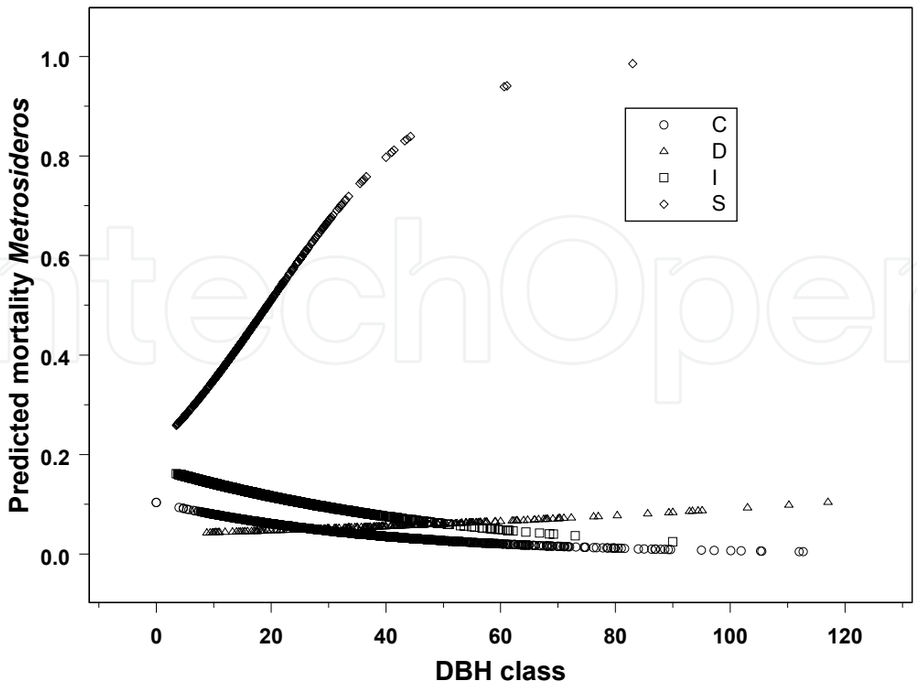

Fig. 2. Predicted mortality of *Metrosideros* from the full logistic model illustrating the interaction between Crown Class (particularly suppressed trees) and DBH. C = Co-dominant, D = Dominant, I = Intermediate, and S = Suppressed.

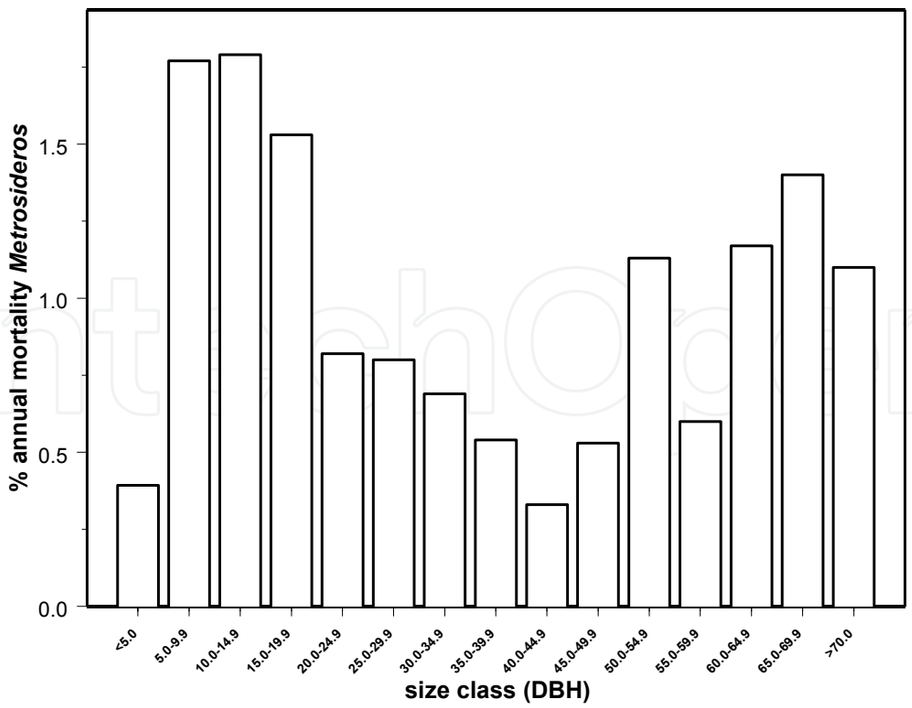

Fig. 3. Percent annual mortality for *Metrosideros* as a function of size class (cm DBH) at Hakalau Forest NWR.

Mortality for *A. koa* showed rather different trends with size. Total mortality during the course of the study for *A. koa* trees in smaller size classes (5-59.9 cm DBH) was 7.6 % (3 out of 39 trees) vs. 15.7 % (11 out of 70) for trees in the larger (> 60 cm) DBH size classes, however this difference was not significant (two-sided Fisher's exact test; P = 0.370). Annual mortality for all size classes of *A. koa* combined was 2.01%; annual mortality of trees below 60 cm DBH was 1.2% vs. 2.4% for those greater than 60 cm DBH.

Of 315 ohia trees between 5-29.9 cm DBH (generally those in the suppressed or intermediate categories) that died during the study period, 55.5% were "dead standing" and presumably victims of competition with neighboring trees, In contrast, of the 78 trees > 30cm DBH that died, only 33.3% were "dead standing. A chi-square test demonstrated a difference in presumed cause of mortality between the large and small size classes ($\chi^2 = 12.35$, df = 1, $P < 0.001$).

Tree age – Approximately one *Metrosideros* tree per ha reaches the age of 650 yrs (range = 590-800 yrs) at Hakalau (Fig. 5). This estimate assumes that the median age of any tree greater than 50cm DBH is 360 yrs, with a range of approximately 300-500 years based on upper and lower 95% Confidence Bounds (Hart 2010) and that the annual mortality rate for these large trees is 1.1% per year.

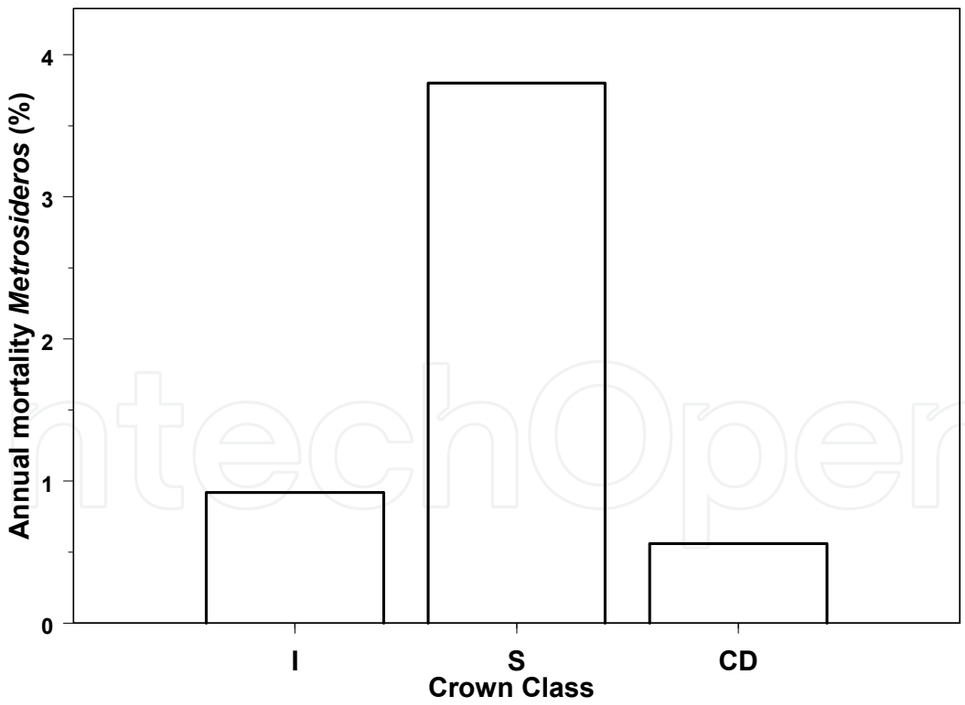

Fig. 4. Percent annual mortality for *Metrosideros* as a function of crown class at Hakalau Forest NWR. Co-dominant and dominant crown classes are combined due to small sample size.

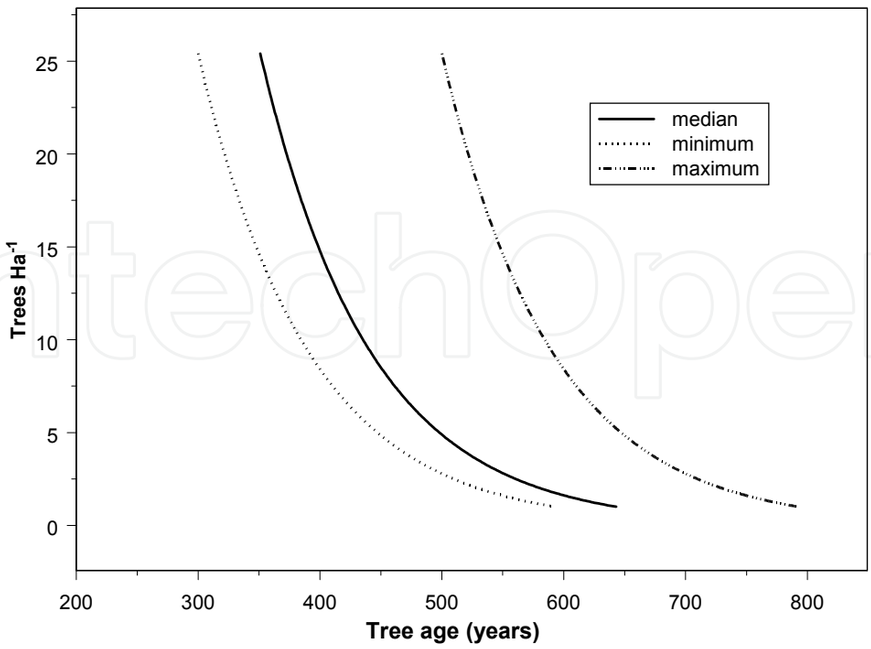

Fig. 5. Prediction curve for tree density (Tree ha^{-1}) vs. age for *Metrosideros* > 50 cm DBH at Hakalau Forest NWR. Assuming an annual mortality of 1.1%, it takes approximately 290 years for the current cohort of 27.1 trees ha-1 >50 cm DBH [with a median age of 360 yrs (range = 300-500 yrs)] to reach a density of 1 tree ha-1.

4. Discussion

Tree mortality patterns in this monodominant forest were somewhat similar to those in far more diverse continental tropical forests. The *forest-wide* annual mortality rate of 1.1% for *Metrosideros* at Hakalau is on the low end of the approximate 1.0 - 2.0 % annual mortality reported for most tropical forests around the globe (Swaine et al. 1987). This mortality rate may be viewed as relatively low especially if one takes into account that *Metrosideros* is dominant across all successional levels, from primary colonizer to late successional "climax" forests (apparently like Hakalau). In most continental forests, primary colonizers have far higher annual mortality, ranging up to 10% and more (Condit et al. 1995). The relatively U-shaped relationship between size and mortality, where intermediate-sized *Metrosideros* individuals exhibited much lower mortality rates than both the smallest and to a certain degree the largest size classes (Fig. 3) also appears to be a common feature of forests, including those from tropical (Korning and Balslev 1994), temperate (Coomes and Allen 2007, Lines et al. 2010), and even sub-boreal (Umeki 2002) regions. However, many other long-term studies in tropical mixed forests (Lieberman and Lieberman 1987; Manokoran and Kochumen 1987; Swaine et al. 1987; Carey et al. 1994) as well as monodominant forests (Nascimento et al. 2007) have reported mortality to be generally independent of size class for trees > 10 cm DBH (but see Clark and Clark 1992).

While it is difficult to disentangle the effects of size vs. crown class on mortality rates due to autocorrelation, examining mortality as a function of crown class is especially revealing. Trees in the suppressed category (those that are competitively inhibited by taller neighbors)

were able to grow slowly, but they suffered by far the highest annual mortality rates (Fig. 4). Conversely, the low annual mortality of 0.56% demonstrated here for the co-dominant and dominant size classes combined indicates that once trees become established in the canopy, mortality is relatively rare. Within this crown class category, the smaller size classes experience mortality rates as low as 0.33% per year, and the largest size classes up to 1.40% per year, possibly due to senescence.

With the exception of studies within *Metrosideros* dieback areas on younger substrates (Gerrish et al. 1988), there has been little previous work on mortality rates of *Metrosideros* trees greater than sapling size in Hawaii. Burton and Mueller –Dombois (1984) found high mortality (57%/yr) for *Metrosideros* seedlings growing in < 5% irradiance, but that annual mortality decreased to 13% for seedlings growing at > 5% irradiance. For trees species other than *Metrosideros*, the mortality data presented here should probably be treated with caution because of low sample sizes. Also, the understory and mid-canopy of the higher elevation sections of the study sites are currently regenerating following disturbance by cattle which should presumably lead to low estimates of mortality for those species that predominate in these layers.

Tree mortality, at both the individual and stand level, is often the result of a combination of abiotic (drought, high winds) and biotic (predation, competition, disease, and senescence) factors. The way in which a tree dies suggests possible factors that contributed to its death (Carey et al. 1994). In this study, there was a significantly higher proportion of trees in the smaller size classes (< 30 cm DBH) than the larger size classes that were classified as "dead standing". These smaller (often intermediate or suppressed) trees that died standing were assumed to be victims of light competition with larger neighbors, with the remainder primarily being killed by neighboring tree falls. This latter process may be important to successional processes in this forest in terms of gap formation. In contrast, large dominant or co-dominant trees that died standing were generally assumed to have senesced. Why might there be a lower proportion of large trees that are dead standing? The answer may be that the heartwood of the largest (>60cm DBH) *Metrosideros* individuals at Hakalau decomposes within a few meters from the ground, presumably predisposing them to treefall as live trees during wind storms, which are common at Hakalau during winter (pers. obs.).

Implications for succession in montane Hawaiian wet forests- The patterns of annual mortality of *Metrosideros* at Hakalau are primarily a function of size and crown class, with suppressed and, to a lesser extent, intermediate trees experiencing much higher mortality rates than co-dominant or dominants. This is the opposite of the majority of Hawaiian wet forests described so far, where the dominant and co-dominant ohia trees that comprise the canopy belong to a similar-aged cohort, with mortality occurring primarily over a relatively short time period as "stand level dieback". As expected, there was also a slight overall increase in mortality as *Metrosideros* reach the largest size classes (Fig. 3), but this senescence occurred on the individual, rather than stand level. With most mortality occurring in the smaller, suppressed classes, these results do not support the cyclic succession model for this forest. Instead, montane wet forests such as the one at Hakalau may be similar to the "Type I" monodominant forests described by Connell and Lowman (1989), in which the dominant species persists through multiple generations. Gap phase dynamics, where large tree falls create openings in the canopy that allow the establishment of seedlings (primarily

Metrosideros) may be an important ecological process that maintains monodominance in large-statured montane wet forests in Hawaii.

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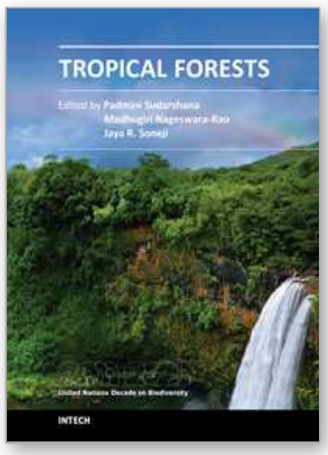

Tropical Forests

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The astounding richness and biodiversity of tropical forests is rapidly dwindling. This has severely altered the vital biogeochemical cycles of carbon, phosphorus, nitrogen etc. and has led to the change in global climate and pristine natural ecosystems. In this elegant book, we have defined "Tropical Forests" broadly, into five different themes: (1) tropical forest structure, synergy, synthesis, (2) tropical forest fragmentation, (3) impact of anthropogenic pressure, (4) Geographic Information System and remote sensing, and (5) tropical forest protection and process. The cutting-edge synthesis, detailed current reviews, several original data-rich case studies, recent experiments/experiences from leading scientists across the world are presented as unique chapters. Though, the chapters differ noticeably in the geographic focus, diverse ecosystems, time and approach, they share these five important themes and help in understanding, educating, and creating awareness on the role of "Tropical Forests" for the very survival of mankind, climate change, and the diversity of biota across the globe. This book will be of great use to the students, scientists, ecologists, population and conservation biologists, and forest managers across the globe.

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